Disentangling the roles of environment and space in ecology

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Most core problems in ecology revolve around variations of the abundance, diversity or metabolic activity of organisms through time and space. Our fundamental questions are: 'Why are there more organisms (or more kinds of organisms, or different kinds of organisms, etc.) here than there?' Although I will focus on abundance in this commentary, the same question can be asked about spatial patterns of diversity, productivity, community structure, body size, etc.

A time-honoured approach to this question is to correlate the variation of abundance with the variation of environmental characteristics. For example, lakes with more phosphorous are greener. Thrips on Australian roses are more abundant when it is hot and wet. And so on. Once identified, correlations beg for a causal explanation. Ideally, controlled experimental manipulations can test hypothesized causal connections between abundance and correlated environmental variables. However, many of the most interesting patterns of nature (abundance gradients, geographical limits to species distributions, latitudinal gradients of diversity, etc.) occur over broad spatial scales. These gradients are often strongly correlated with environmental variables such as precipitation or temperature. Causal explanations of the correlations have been proposed, but experimental tests at these scales are rarely an option.

So do environmental gradients really cause broad-scale biotic gradients? A growing literature suggests that at least part of the spatial variation in abundance, richness, etc. may be due to spatial autocorrelation: the biology of sites close to one another tends to be more similar than that of sites far apart. Spatial autocorrelation first caused concern because it causes a form of pseudoreplication (Legendre, 1993). Closely spaced samples may essentially be replicate measures of the same conditions, such that they do not each contribute a full degree-of-freedom to statistical analyses. Hypothesis tests then become too liberal. This is often just a nuisance: adjusting the number of degrees of freedom can correct the problem (Rangel et al*.,* 2006). However, depending on how it arises, autocorrelation can also theoretically affect the observed shape of abundance–environment relationships.

If autocorrelation in abundance is *exogenous*, resulting from environmental drivers that are spatially structured (Fig. 1a, arrow 1), then traditional, non-spatial statistics describe the abundance–environment relationship perfectly well. Creatures are more abundant here, vs. there, because here it is hotter, or wetter, or there is more phosphorous. Troubles arise if autocorrelation is *endogenous*, arising from the biology of the creatures in question. For example, metapopulation dynamics could make close populations more similar in abundance than far ones (Fig. 1a, arrow 3), creating spatial patterns of abundance irrespective of environmental gradients. But would these patterns confound abundance–environment relationships? I have generally thought (Fig. 1b) that space structures environmental variables, which then structure populations, but that endogenous spatial autocorrelation is probably relatively inconsequential over broad spatial scales because population processes are fairly local.

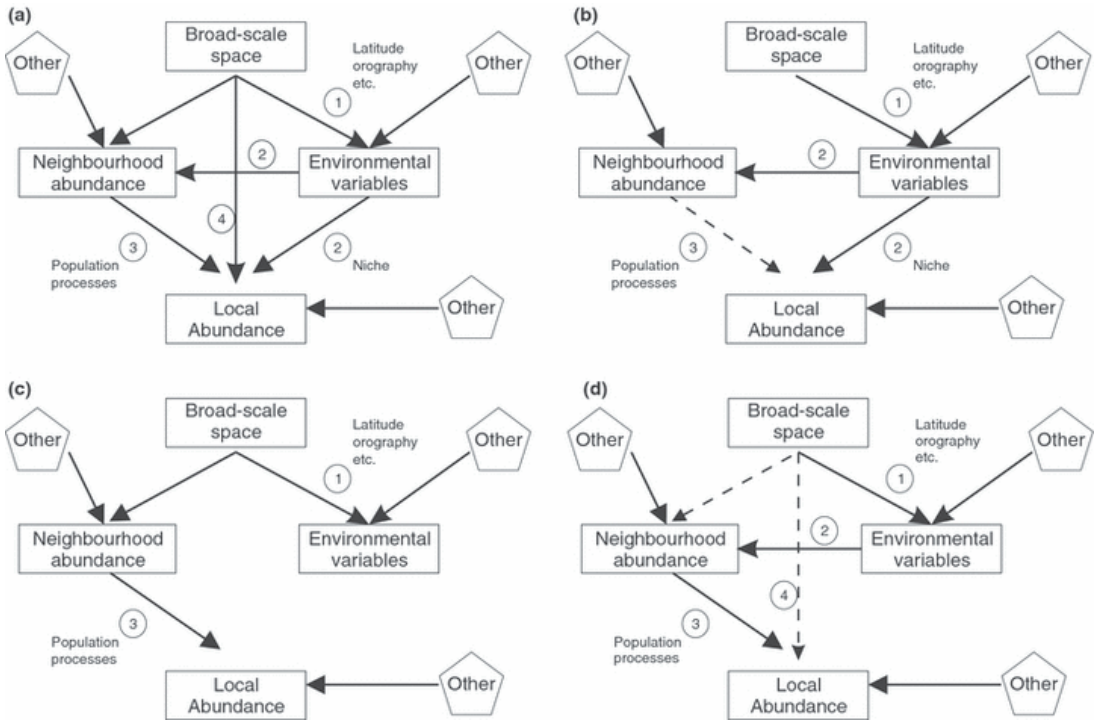

Figure 1. Conceptual causal models of influences on local population abundance. (a) A set of possible interactions. 'Broad-scale space' refers to any processes that would give rise to spatial autocorrelation over long distances. 'Neighbourhood influences' refer to the influence of populations within a 200-km radius. Environmental variables include climatic variables, edaphic variables and variables that affect primary productivity. (b) The author's preconception of what is likely to be true. (c) This model suggests (as Bahn & McGill, 2007) that environmental variables do not directly influence population abundance; rather, broad-scale spatial autocorrelation structures both environmental variables and abundance in similar manners in space. (d) This model may also be consistent with Bahn & McGill's results. In this view, environment structures neighbourhood abundance, and other population processes further structure local abundance.

Bahn & McGill (2007) recently asked a clever question that upset my complacency: what if environmental variables predict spatial variation in the abundance of organisms because the two have similar spatial structures, and *not* because environment actually influences abundance? To address this question, they used 190 widespread species from the North American Breeding Bird Survey. They compared observed variation in abundance with the predictions of three models. The first was a typical niche model: abundance as a function of environmental (mainly climatic) variables. Their niche model should capture direct effects of the environment, whether spatially structured or not (Fig. 1, arrow 2). A second model related abundance to geographical coordinates (latitude and longitude).

This model would presumably capture environmental effects that show long autocorrelation (Fig. 1, arrow 4 plus arrows 1→2 and 1→2→3). A third model related local abundance to the distance-weighted abundance of conspecifics at sites within 200 km, which would capture short-distance autocorrelation in abundance, both exogenous and endogenous (Fig.1, arrow 3). Bahn & McGill found that variation in avian abundance can plausibly be related entirely to spatial autocorrelation! Latitude and longitude statistically accounted for just as much variance in bird abundances as did the environmental variables. Combining environment and latitude/longitude explained no more.

Thus, the variation in abundance that is related to geographical coordinates is indistinguishable from the variation that can be related to environmental variables. The average abundance of neighbours was an even stronger predictor of local abundance. Consequently, spatial interpolation outperformed niche models, irrespective of environmental gradients. Bahn & McGill also constructed artificial species ranges, centred randomly in North America, and assuming Gaussian distributions of abundance in space. Environmental variables predicted the variation in abundance in simulated ranges nearly as well as in real ranges, even though there is clearly no causal relationship between environment and a simulated range.

Thus, Bahn & McGill's data appear to be consistent with a simple, disturbing hypothesis (Fig. 1c): abundance–environment correlations may simply result because both variables are similarly structured in space. The direct effect of environment on local abundance may be very small. Rather, neighbourhood abundance may determine local abundance. Consequently, simple interpolation yields good predictions of abundance. But this is an extreme interpretation. Even Bahn & McGill do not suggest that spatial variation in abundance contains no environmental signal at all. One might even argue that Bahn & McGill's results show nothing that we did not already know. Sites close in space tend to be environmentally similar.

Biotic processes such as dispersal make ranges more-or-less continuous. So it is entirely predictable that neighbouring abundances should be similar too. But autocorrelation (and interpolation) cannot explain why abundance, both here and nearby, is n, vs. $2n$ or $n/2$. Abundance–environment relationships do (potentially) explain that variation. There are techniques designed to examine statistical relationships in the presence of autocorrelation (e.g. Lennon, 2000; Fortin & Dale, 2005), which Bahn & McGill did not use. However, most of these models test for a marginal effect of environmental variables, after controlling for autocorrelation. In essence, they first interpolate abundance, and then test for environmental effects.

If spatially structured environmental variables control abundance, they will induce exogenous autocorrelation, and methods that control for autocorrelation will mask the environmental effects. We are no farther ahead in distinguishing effects of environment vs. endogenous autocorrelation on abundance. I suspect that Bahn & McGill's data are also consistent with a model in which environment determines neighbourhood abundance, and population processes modify abundance locally (Fig. 1d). I think this because the space-only model (Fig. 1c) cannot explain why niche modelling successfully predicts abundance in disjunct areas, or why ranges shift when climate changes. The practical utility of interpolation as a tool to predict abundance falls off rapidly with distance, whereas niche models do not necessarily do so.

Bahn & McGill's work seems both cautionary and promising. First, they question to what extent biology–environment relationships exist because the variables depend similarly upon space, rather than because biology depends upon environment. Explanations of global-scale patterns of species richness face the same problem. Richness typically varies fairly smoothly (i.e. has positive autocorrelation) over long distances (e.g. H-Acevedo & Currie, 2003) as do climatic variables.

Perhaps richness correlates strongly with climatic variables at this scale because their autocorrelation structures are similar (Lennon, 2000). Storch *et al.* (2006) and Rahbek *et al.* (2007) recently showed that some of the variance in broad-scale variation in species richness results from the fact that species ranges are typically spatially continuous over long distances. In other words, empirically, autocorrelation accounts for some of the variance in species richness. Second, Bahn & McGill's work suggests an opportunity. The notion that environment has little direct effect on broad-scale variation in abundance will be quite indigestible to many ecologists. Yet, the processes that give rise to spatial autocorrelation appear to provide better predictive power than current non-spatial models can offer. A challenge for the future will be to exploit this largely untapped source of information.

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